

A Contribution to the Gametophyte Morphology and Development in Several Species of *Thelypteris*, Thelypteridaceae

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ABSTRACT.—A contribution to the study of the gametophyte's morphology and development of some species of *Thelypteris* Schmidel (Thelypteridaceae). The development and morphology of the sexual phase of five species of the Thelypteridaceae family is described and compared. Spores were sown in Thompson medium with agar, germination occurred after 11 days; all spores of the species studied are monolete, ellipsoid with a pleated perine, brown to dark brown; the germination pattern is *Vittaria* type and the prothallial development is *Aspidium* type. Gametangia are of the common type of the leptosporangiate ferns. Sporophytes in *Thelypteris reptans* var. *reptans* and *T. tetragona* appear 90–285 days after sowing; *T. dissimulans*, *T. piedrensis* and *T. oviedoae* did not develop any sporophytes. The sexual phase of these species has many morphological characteristics in common with species of the Old and New Worlds.

The genus *Thelypteris* has *ca* 1000 species distributed in tropical and subtropical regions; the American species have been taxonomically studied by Smith (1971, 1973, 1974, 1980). Approximately 300 species are found in Neotropical areas, *ca* 60 of which are known from Mexico (Smith, 1973, 1974, 1995). Some pteridologists have subdivided *Thelypteris sensu lato* into natural groups as genera, subgenera or sections. Many of the New World taxa can be circumscribed using different combinations of characters and thus be treated as genera. In this paper we treat *Thelypteris* in the broad sense, but recognize several subgenera.

As construed, *Thelypteris* is distinguished by the presence of two vascular bundles in the petiole (*Dryopteris* and other closely related groups have many vascular bundles), acicular hairs on many parts of the blade, spores usually bilateral with a prominent perispore, and a chromosomal base number of 27 to 36 ($x = 40, 41$ in *Dryopteris*, *Athyrium*, and close relatives).

Although the determination of the Thelypteridaceae is based on the sporophyte's morphological characters such as, mainly, the type of indument, for example: bifurcated or stellate hairs (subg. *Goniopteris*); acicular, unicellular or pluricellular hairs (subg. *Goniopteris*), stellate or no furcate hairs (subg. *Macrothelypteris*; subg. *Meniscium* and subg. *Amauropelta*); setose sporangia (subg. *Stegnogramma*); sporangia without setae (subg. *Cyclosorus*, and subg. *Steiropteris*), when doing a follow up of the morphogenetic development, we would expect to find that the gametophytes have the same type of indument, a diagnostic character that would help us to support the segregation at the subgeneric level. Nevertheless, in the studied species we could only observe in the laminar phase, unicellular, capitate hairs, with

a waxy secretion. For this reason we suggest a more detailed study with a larger number of species in order to learn if the indument is a useful character, helpful in separating the species into well defined subgenera, or to join them in infraspecific taxa. Details of the plants' indument provide important taxonomic characters. The indument includes: sessile or pedicellate stellate hair, bifurcate hairs, anchor shaped, fasciculate or hooked hairs; sessile or stipitate glands, setose sporangia or sporangia with stellate hairs or glands. We would expect the plant's gametophytes to share these characteristics.

Although the Thelypteridaceae is very large, its prothallial morphology is poorly known. Its gametophytes can be described as follows: epigeous, chlorophyllous, at maturity cordiform or elongated-cordiform, symmetrical, often with wide wings, fast growing, without a thickened cushion or lacking one, with colorless or light brown rhizoids abundant on the cushion's ventral surface, frequently with unicellular hairs or rarely pluricellular and/or glandular hairs on the margin and on both surfaces. Gametangia are of the advanced leptosporangiate type: the antheridia are characteristically three-celled and dehiscence occurs when the opercular cell detaches; the archegonia are ventral surface, especially on the lower region, the slim neck points towards the meristematic notch (Tryon and Tryon, 1982).

Previous work on *Thelypteris* gametophytes, mainly Asian species include: Schmelzeisen (1933), Momose (1938, 1941), Kachroo (1963), Nayar and Chandra (1963, 1965, 1966), Chandra and Nayar (1968), Devi (1966), Nayar and Devi (1963, 1964), Nayar and Kaur (1969), Mitra and Sen (1981) and Tigerschiöld (1989a, 1989b, 1989c, 1990). Details on the prothallia of New World *Thelypteris* are mentioned by Stokey (1960), Atkinson (1971, 1973, 1975a, 1975b), Atkinson and Stokey (1964, 1973). Huckaby and Raghavan (1981b) worked with 16 Jamaican species; Reyes-Jaramillo and Pérez-García (1991) worked with *T. patens* and *T. puberula* var. *puberula*; Pérez-García *et al.* (1994) worked with *T. rhachiflexuosa* and Nester-Hudson *et al.* (1997) worked with *T. ovata* var. *lindheimerii*.

This paper is a contribution to the study of the morphology and development of the gametophytes of *Thelypteris* (*Amauropelta*) *pedrensis* (C. Chr.) Morton, *T. (Cyclosorus) oviedoae* C. Sánchez & Zavaro, *T. (Goniopteris) dissimulans* (Maxon & C. Chr. ex C. Chr.) C. F. Reed, *T. (Goniopteris) reptans* (J.G. Gmelin) Morton var. *reptans* and *T. (Goniopteris) tetragona* (Sw.) Small.

MATERIALS AND METHODS

Material for research was collected from the "Jardín Botánico de los Helechos", in Santiago of Cuba and from several different Cuban localities (Table 1). Vouchers are kept at this Herbarium (BSC). Spores were obtained from the fertile leaves of different individuals and leaves with spores were kept in paper envelopes to be released at room temperature. The samples were put through a metallic sieve, with pores 0.074 mm in diameter to remove excess non-spore material. Spores of each species were sown, without sterilization, in 5 Petri dishes, 5 cm in diameter (3 replicates for each species), onto Thompson

TABLE 1. Sites of origin of the taxa under research. Caluff = Manuel García Caluff; Shelton = Gustavo Shelton Serrano, all vouchers have been deposited alive at the BSC (Fern Garden), Santiago de Cuba, Cuba.

Taxa	Vouchers	Locality	Habitat/Altitude
<i>Thelypteris</i> (<i>Goniopteris</i>) <i>dissimulans</i>	Caluff & Shelton 4204	Margins of the "Barao del Banao" river, Santispiritus, Prov. de Santispiritus, Cuba	Gallery forests on limestone rocks, 250 m asl
<i>Thelypteris</i> (<i>Amauropelta</i>) <i>piedrensis</i>	No date	"Jardín de los Helechos" (Fern Garden)	No date
<i>Thelypteris</i> (<i>Goniopteris</i>) <i>reptans</i> var. <i>reptans</i>	Caluff & Shelton 2963	Mogotes of boigne, La Tabla, 3er frente, Prov. de Santiago de Cuba, Cuba	Perennial vegetation, on limestone rocks and slopes, 600 m asl
<i>Thelypteris</i> (<i>Goniopteris</i>) <i>tetragona</i>	Caluff 47 A-B	Altos de Villalón, "La Gran Piedra" mountain range, Prov. Santiago de Cuba, Cuba	Secondary growth, coffee plantations, 500 m asl
<i>Thelypteris</i> (<i>Cyclosorus</i>) <i>oviedoae</i>	Caluff s/n	"Lomas del Solón", las Terrazas, Prov. Pinar del Río, Cuba	Secondary growth on road margins, 600–650 m asl

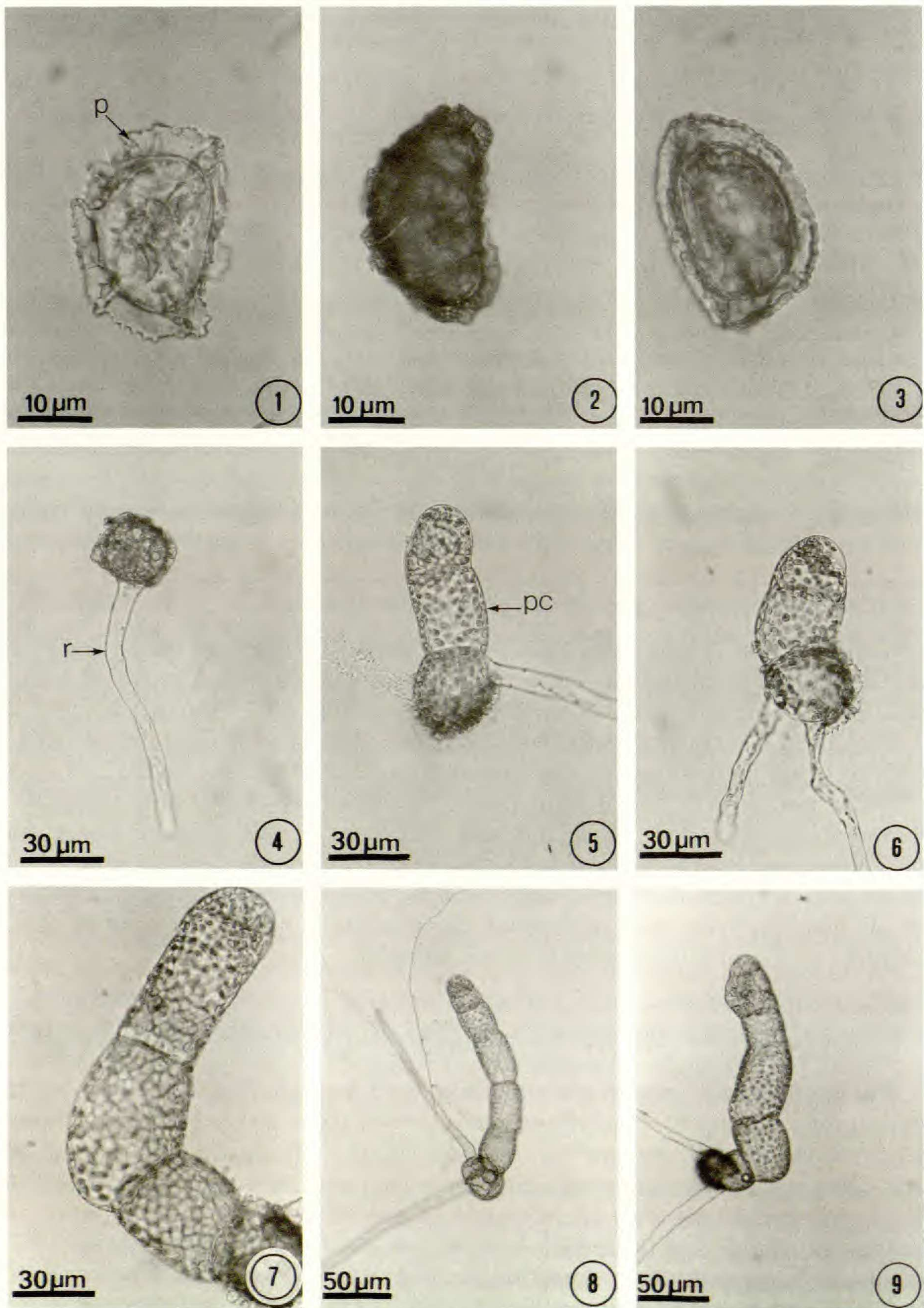
sowing medium (Klekowski, 1969), under aseptic conditions into 5 cm Petri dishes; spores were spread across the medium surface with a brush of scarce bristles. The density of the sown spores varied from 100–150/cm².

The cultures were kept under lab conditions inside transparent polyethylene bags to avoid contamination and dehydration, under a 12 hr light/12 hr dark photoperiod, with artificial light (Solar 75 Watts, day light) and a 25–28°C temperature. One dish of each taxon was kept in the dark to check for photoblastism. Spores of the five species were also sown separately in soil in 3 small pots, 5 cm in diameter (2 replicates for each species). Photomicrography of all gametophytes was performed on specimens grown on agar in Petri cultures and sporophytes grown in soil samples.

RESULTS

The spores of all species are monolete, with a single leasura and brown to dark-brown. Spores of *T. piedrensis* measure 45 µm × 29 µm (51 µm × 30 µm) 55 µm × 32 µm, of *T. reptans* var. *reptans*, 50 µm × 30 µm (52 µm × 34 µm) 58 µm × 38 µm, of *T. tetragona* 42 µm × 28 µm (44 µm × 29 µm) 47 µm × 32 µm, of *T. dissimulans* 48 µm × 30 µm (49 µm × 33 µm) 50 µm × 35 µm, the perine can be wide or narrow and it has various ornamentations. In *T. dissimulans* (Fig. 1) the perine is quite thick, in *T. piedrensis* (Fig. 2) and *T. oviedoae* it is very thin, and in *T. reptans* var. *reptans* (Fig. 3) and *T. tetragona* it is intermediate in thickness.

In all species germination began 8–11 days after sowing. Germination is first evidenced by the development of the very long, hyaline rhizoidal cell



FIGS. 1–9. Monolete spores, germination and filamentous phases of *Thelypteris*. Fig. 1–3. Spores. 1. *T. dissimulans*. 2. *T. piedrensis*. 3. *T. reptans* var. *reptans*. 4. Germination in *T. reptans*, (11 days). 5–9. Filamentous phases. 5. *T. dissimulans* (26 days). 6. *T. tetragona* (11 days). 7. *T. piedrensis* (14 days). 8. *T. oviedoae* (15 days). 9. *T. piedrensis* (14 days). p = perine, pc = prothallial cell, r = rhizoid.

containing limited cytoplasm and the prothallial cell which develops inside the spore coat (Fig. 4). This type of germination is the *Vittaria*-type, characterized by the first division giving rise to an initial rhizoid oriented perpendicular to the long axis of the spore. The second division produces an initial prothallial filament at the base of the rhizoid but at right angles to it (Fig. 5).

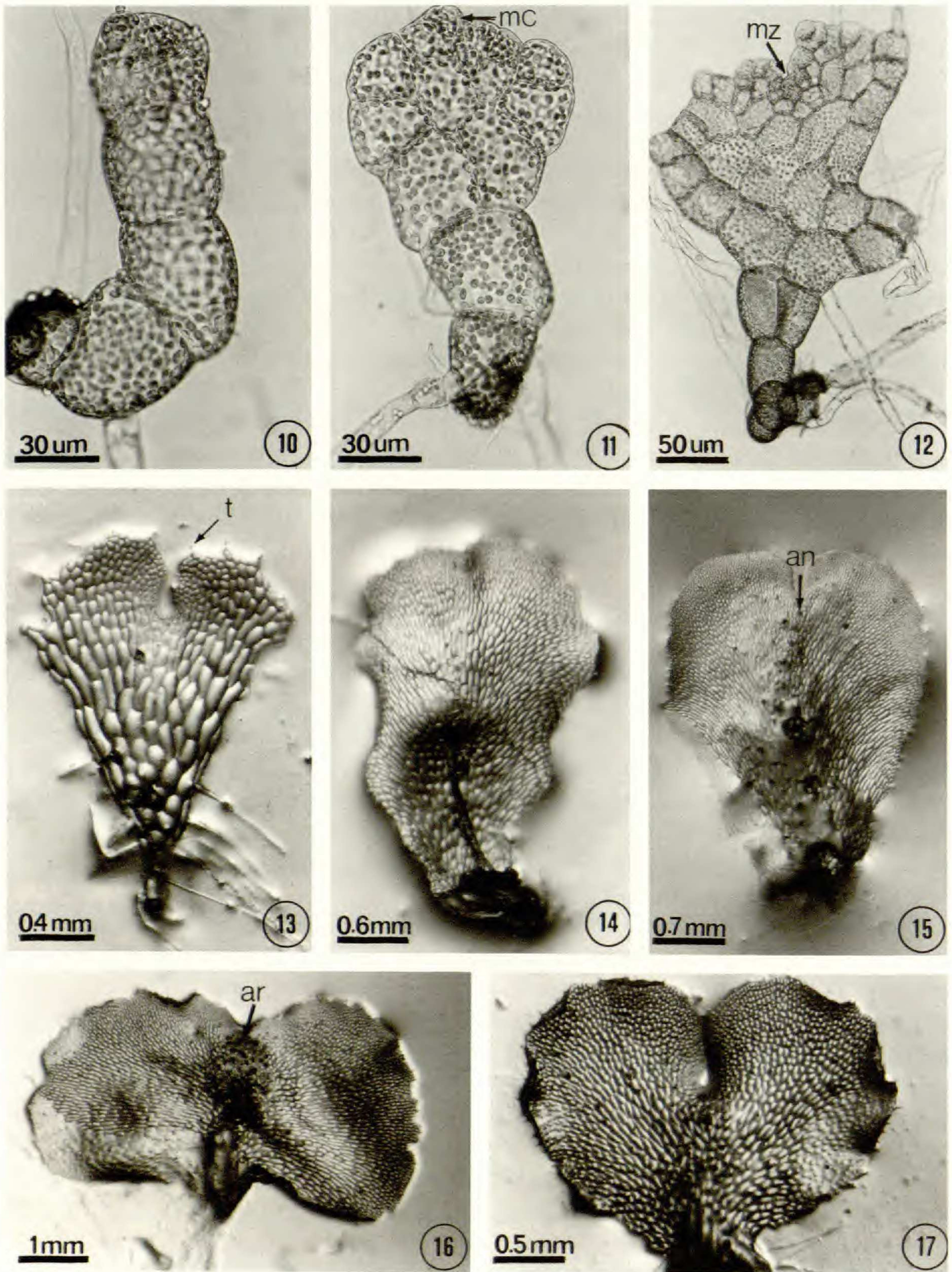
The filament phase begins between days 11 and 26. During this phase a sequential series of cell divisions occur in essentially the same plane to produce a slim, pluricellular germinal filament of three to seven barrel shaped cells (Figs. 5–9). All of these prothallial cells have numerous chloroplasts. This uniseriate condition is only a temporary phase. *Thelypteris oviedoae*, *T. piedrensis*, *T. reptans* var. *reptans* and *T. tetragona* have the same development period of 11–15 days; the development of this phase takes longer in *T. dissimulans* (11–26 days).

The development time of the plate phase varies among species: in *T. oviedoae* and *T. piedrensis* it is 26–50 days long, in *T. reptans* var. *reptans* and *T. tetragona* 26–60 days, and for *T. dissimulans* it is 70 days. All species have an *Aspidium*-type prothallial development (Fig. 10–13), in which the uniseriate filament and plate phase development begins before the appearance of hairs, the meristematic cell is located centrally (Fig. 11) along the distal margin, the prothallus grows due to this cell's activity and later acquires a notch and becomes apical, a pluricellular meristem becomes apparent and, later, a cushion develops; young prothallia begin to grow unicellular (Fig. 12), capitate hairs.

The *Aspidium*-type is variable with regard to sequence of cell divisions. The sequence of cell divisions and development of the young thallus are conditioned here by early hair formation in the young prothalli. Plate phase formation is initiated by cells behind the terminal cell (sometimes the penultimate cell of the germ filament in also sluggish) dividing longitudinally. Marginal hairs are produced continuously.

The prothallus grows by the activity of the meristematic cell and soon the meristematic region becomes notched and apical by unilateral growth of the thallus. A pluricellular meristem is established in the usual way and soon afterwards a midrib is formed. The mature prothallus is cordate and profusely hairy.

The adult phase corresponds to days 60 to 150 in *T. reptans* var. *reptans* and *T. tetragona*. It has a cordiform-spatulate shape with an indistinct notch, an elongated, thickened cushion over which the gametangia and rhizoids are found, and short, more or less isodiametric, undulating wings with marginal and superficial capitate hairs (Figs. 14–15). There is variation in the shape of the gametophyte in *T. oviedoae* and *T. piedrensis* (50–75 days), *T. reptans* var. *reptans* (80–150 days), and *T. dissimulans* and *T. tetragona* (60–200 days) where the gametophytes have a cordiform-reniform shape, with a dense cushion, a marked notch, wide and isodiametric wings, with undulate margins and the same type of hairs (Figs. 16–17). Rhizoids of all gametophytes are ventral, unicellular, hyaline to light brown, and abundant, intermixing with the reproductive structures.



FIGS. 10–17. Developmental stages of the gametophytes of *Thelypteris*. 10–13. Young plate phases. 10. *T. piedrensis* (15 days). 11. *T. tetragona* (15 days). 12. *T. tetragona* (26 days). 13. *T. piedrensis* (32 days). 14–17. Adult gametophytes, spatulate to cordiform. 14. *T. tetragona* (89 days). 15. *T. tetragona* (70 days). 16. *T. reptans* (89 days). 17. *T. piedrensis* (50 days). an = antheridia, h = secretory hairs, mc = meristematic cell, mz = meristematic zone.

According to Atkinson, thelypteridoid ferns are generally characterized as having pubescent gametophytes; glabrous gametophytes have never been observed. Hairs are commonly simple and non-chlorophyllous, with a yellow or transparent secretion. Hairs of the studied species were found on the margin and on both surfaces of the gametophyte; they are hyaline unicellular, and capitate, with an extracellular waxy coat on the apex (Figs. 18–19). These hairs develop during the young plate phases in *T. oviedoae* and *T. piedrensis*, in *T. reptans* var. *reptans* at 26 days and in *T. dissimulans* and *T. tetragona* at 35 days. They are abundant on the adult phase, and are distributed along the margin and on both surfaces.

The gametangia are characteristic of typical leptosporangiate ferns. Archegonia are located distally on the cushion intermingled with the rhizoids. The long neck, which is oriented toward the meristematic zone, is composed of four rows of neck cells and a mouth of four cells (Figs. 20–21). Archegonia develop in *T. reptans* var. *reptans* at 67–75 days, in *T. piedrensis* at 89 days and in *T. tetragona* at 70–108 days. The antheridia are small, globose, with a basal cell, an annular cell and an opercular cell (Figs. 22–23). They develop in *T. tetragona* at 70–108 days, in *T. piedrensis* at 89 days and in *T. reptans* var. *reptans* at 67–108 days. Gametangia did not develop in either *T. dissimulans* or *T. oviedoae* during the 300 days of cultivation.

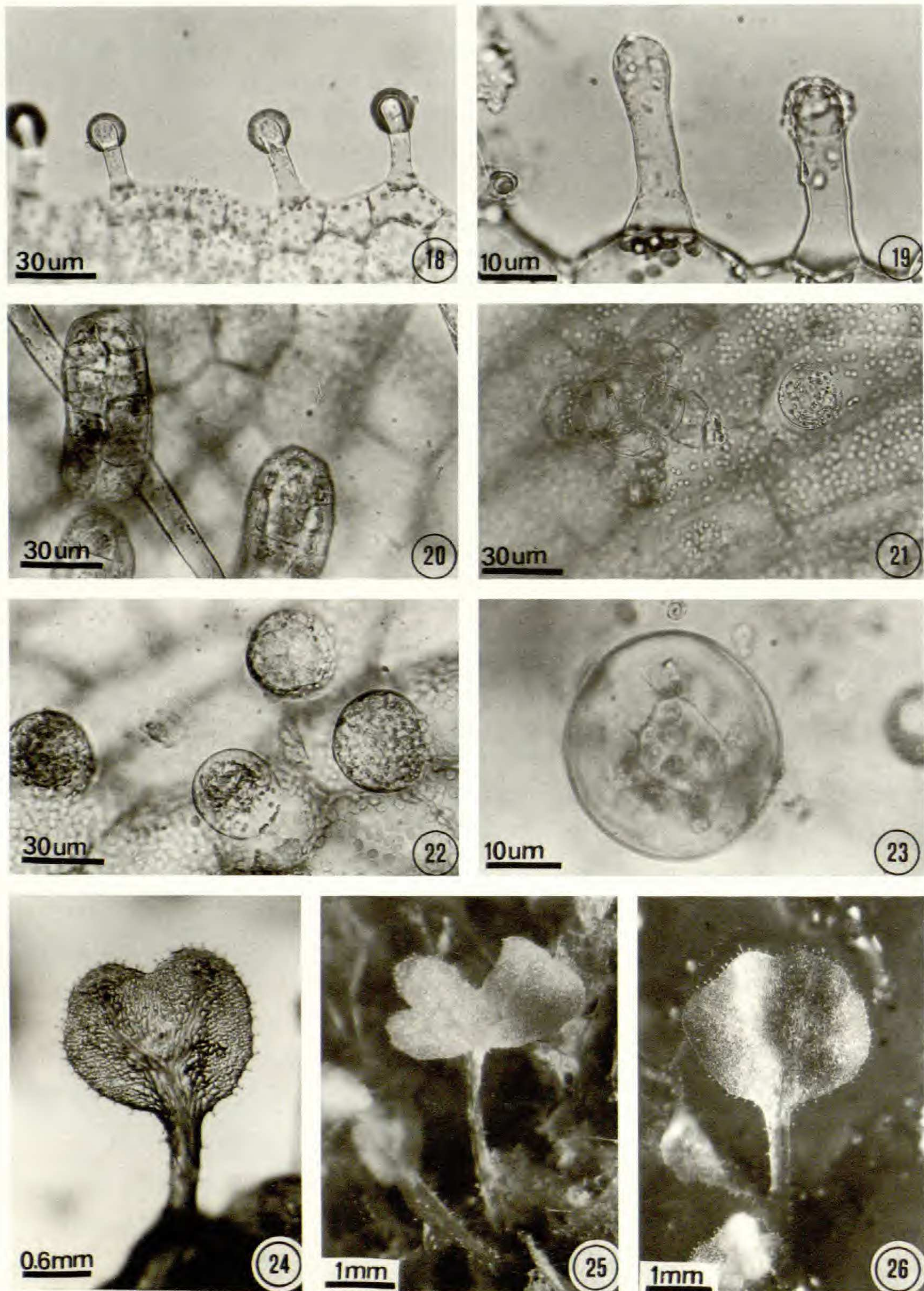
Sporophyte initiation was observed in *T. tetragona* at 89–166 days, and in *T. reptans* var. *reptans* at 137–285 days. Sporophytes did not develop in cultures of *T. dissimulans*, *T. piedrensis* or *T. oviedoae*, even after 300 days of cultivation.

First leaves of young sporophytes had a petiole and a 2-, 3-, or 4-lobed blade. The venation was open and dichotomous (Figs. 24–26). All leaves had abundant hairs, marginally and on both surfaces. The hairs were unicellular, capitate, hyaline, achlorophyllous and secretory, similar to those on young and adult gametophytes. Stomata are of the polycitic-type, with one or two subsidiary cells (Kondo, 1962; Thurston, 1969; Smith, 1990).

DISCUSSION

All spores are monolete, with ornamentation ranging from reticulate-pitted in *Thelypteris* subgenus *Amauropelta*, to winged in *T.* subgenus *Goniopteris*, to low ridged or ridged-papillate in *T.* subgenus *Cyclosorus* (Wood, 1973; Tryon and Tryon, 1982; Tryon and Lugardon, 1991).

The gametophyte phase of the Thelypteridaceae, especially subgenera *Amauropelta*, *Cyclosorus*, *Goniopteris* and *Thelypteris*, is notoriously uniform, both in relation to spore germination, the *Vittaria*-type (Nayar and Kaur, 1971; Huckaby and Raghavan, 1981a) and prothallial plate development, the *Aspidium*-type. In the *Vittaria*-type germination, the spore's first division produces two unequal cells, a smaller one that immediately elongates and differentiates into the first rhizoidal cell, and a second larger cell which eventually gives rise to cells of the prothallial plate.



FIGS. 18–26. Secretory hairs, gametangia and first leaves in *Thelypteris*. 18–19. Unicellular secretory hairs. 18. *T. piedrensis* (89 days). 19. *T. reptans* (75 days). 20–21. Archegonia. 20. Neck of archegonia in *T. reptans* (67 days). 21. Mouth of archegonia in *T. tetragona* (70 days). 22–23. Antheridia. 22. *T. reptans* (67 days). 23. *T. tetragona* (108 days). 24–26. First sporophyte leaves. 24. *T. reptans* (137 days). 25. *T. tetragona* (166 days). 26. *T. reptans*. (166 days).

Seven different types of prothallial development in the homosporous ferns are described by Nayar and Kaur (1969). The critical elements which define these types are differences in the sequence of cell divisions during development, the location at which a meristematic cell or pluricellular meristem is established, and the ultimate shape of the thallus.

Although the taxa studied by us show a delay in prothallial hair development according to Nayar and Kaur (1969), we consider that they have an *Aspidium*-type development because the meristematic cell has a very active role in the growth and expansion of the young prothallus and this *Aspidium*-type of development is seen in more advanced genera such as *Thelypteris*.

During the each developmental stage, the plate of the gametophyte originates from three divisions on the same plane - two lateral and one horizontal - of the inferior face of an initial meristematic cell. That cell is subsequently replaced by a group of meristematic cells which contribute to the development of the cushion and to the expansion of the gametophyte wings. The substitution of the initial cell by a pluricellular meristem is common in other subgenera of *Thelypteris* (Kachroo, 1963; Nayar and Chandra, 1963; Atkinson, 1971; Reyes-Jaramillo and Pérez-García, 1991).

A distinctive characteristic of the gametophytes of the different subgenera of the Thelypteridaceae is the differentiation of unicellular, short, capitate hairs, with a wax secretion at the apex, during the blade development. This was clearly seen in all species.

Various authors have studied the gametophyte morphology of various species of Thelypteridaceae. They are all pubescent, with a relatively long-lived thallus that become cordate at maturity, delicate for their size, with a cushion and wide wings, abundant colorless or light brown rhizoids and advanced-type sexual organs. Although the differences regarding spore ornamentation, length of simple hairs and antheridia shape are insignificant, these characteristics vary in different species; the taxa we studied share the characteristics previously mentioned. We summarize that the morphology of the gametophytes in *Thelypteris* have a *Vittaria* type germination pattern, an *Aspidium* type prothallial development, that the gametophytes are generally uniform in form and development, and show enough diversity to suggest that they are useful in understanding taxonomic boundaries.

In the species studied here we only observed the most common type of hair, which is unicellular, capitate, secretory and with a waxy secretion; we did not observe other types of hairs mentioned in the literature, for example, secretory hairs, long, glandular-septate hairs, and acicular hairs (Kachroo, 1963; Nayar and Kaur, 1971; Tigerschiöld, 1989b, 1990).

Prothallial hairs have developed only in some subgenera, possibly the presence of similar types of hairs in groups apparently unrelated gave origin to the idea that epidermal derivatives are of little value in taxonomic and phyletic studies. Nevertheless, the restricted distribution of pubescent gametophytes among several phyletic groups, and the presence of certain characteristic types of hairs in other groups (for example: acicular hairs in the Thelypteridaceae) apparently indicate that these are important characteristics in comparative

studies. As is common with other aspects of gametophyte morphology, the tendency to have hairs seems to have developed independently in the different phyletic groups of ferns.

Regarding the gametangia, our results indicate that the antheridia have the characteristic type of structure and ontogeny characteristic of advanced ferns such as the Thelypteridaceae (Davie 1951) and Stone (1960). Tigerschiöld's (1989a) contributions in which she mentioned four different dehiscence types in antheridia: 1) irregular split on the wall of the opercular cell, 2) a circular split similar to a pore, 3) the opercular cell is expelled completely to the exterior and 4) the slit opens laterally (like a lid), the operculum remains joined to the annular cell. Although it has been stated that dehiscence is specific to each species, Tigerschiöld (1989a) observed that this is not always true, the same species can have two or three of these dehiscence mechanisms. All of the gametophytes in this study dehisced by means of the separation of the whole opercular cell, which in this case corresponds to Tigerschiöld's type three. In other studies, Tigerschiöld (1989b, 1990) showed that his thelypteroid ceylandes gametophytes are similar in most respects.

Nevertheless, we did find some distinguishing characteristics among the species. Variation was present in thallus margin shape, hair length, abundance of secretory hairs, presence or absence of acicular hairs, number of archegonial neck cells, and opercular cell form. Just as antheridial anthesis and antherozoid liberation varies in each of the species studied, this study demonstrates that it is possible to identify species based on characteristics of the gametophyte alone.

Stokey (1951), Atkinson and Stokey (1964) and Smith (1971) state that fern gametophytes have only recently begun to be considered as a possible source of taxonomic characters, or as a comparative morphological tool. Gametophytes seem to be useful in systematics at the family level, and in certain cases, at the generic level, but they are most frequently used, on a smaller scale, to distinguish species within the same genus.

The gametophyte's uniform development in species of different subgenera of the Thelypteridaceae has been mentioned by several authors (Nayar and Chandra, 1963; Huckaby and Raghavan, 1981a; Tigerschiöld, 1989a, 1989b, 1990; Reyes-Jaramillo and Pérez-García, 1991). Nevertheless, the comparative study of the gametophyte development of American species helps define, based on hair type and position, margin, antheridial structure and shapes of the antheridial slit, the combination of characters that will delimitate subgenera, species, or groups of species within the Thelypteridaceae (Atkinson 1973; Pryer *et al.*, 1995).

This study of the gametophytes of five species of thelypteroid ferns from the New World indicates that they can be very diverse and that they are distinctive. Nevertheless, because the sampling was scarce, this conclusion could be premature or it could only represent a record of the gametophyte's characteristics and an effort to accommodate or adjust them within today's classification. This research could be useful as a comparative basis in which many thelypteroid gametophytes could begin to be known.

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